# THE INTERRELATIONSHIPS OF SOME CRETACEOUS CODIACEAE (CALCAREOUS ALGAE)

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ABSTRACT. The anatomy and evolution of fossil codiacean calcareous algae referred to *Arabicodium* and *Boueina* (Jurassic–Cretaceous) and *Halimeda* (Upper Cretaceous–Recent) are discussed. It is considered that all are referable to one botanical genus *Halimeda*; differentiation of the earlier species-groups (*Boueina* and *Arabicodium*) was followed by hybridization and selection in the Upper Cretaceous, leading to *Halimeda* s.str., a group of species of more vigorous growth and showing a combination of characters from the older species-groups.

THE genus *Halimeda* (Chlorophyta, family Codiaceae) is one of the most successful of modern warm-water marine algae. It abounds in clear shallow lagoonal and coastal waters throughout the tropical and subtropical areas of the Indo-Pacific, and the Atlantic with its adjacent Caribbean and Mediterranean. Since the segments of internodes of the *Halimeda* fronds are usually heavily calcified and growth of the plants is rapid, it is an important sediment-former, as directly evidenced by borings on atolls (Hinde 1904, Johnson 1961). Throughout the Tethyan area remains of *Halimeda* are common in the appropriate facies of Tertiary limestones, and segments of similar forms to those of some of the Recent species are known from rocks as old as the Eocene (e.g. *H. eocaenica* and *H. praemonilis*; Morellet and Morellet 1941). The origin of *Halimeda* is clearly pre-Tertiary.

### SOME CRETACEOUS CODIACEAE

Segmented codiaceae in the Cretaceous are represented by assemblages of dissociated segments which have been referred to three genera: Arabicodium, Boueina, and Halimeda. Although typical segments for each differ in size and shape, and in internal thread-detail, they all agree in possessing longitudinal medullary threads and a zone of more or less radial cortical threads, and it seems reasonable to conclude that they came from plants of similar general morphology to that of the living Halimeda, and of close relationship to it. This was suggested for Boueina and Halimeda by Steinmann (1899) and Pia (1926, 1927). Boueina and Arabicodium have Lower Cretaceous type species, and are represented earlier in the Jurassic. Halimeda does not appear before the Upper Cretaceous. There are also numerous Cretaceous species from Aptian to Senonian, which are difficult to assign conclusively to any of the three genera since they show intermediate characters.

Boueina (type species: B. hochstetteri Toula 1884 from the Lower Cretaceous of Serbia) shows elongate cylindrical segments, circular in cross-section, and not flattened or branched as are those of most Tertiary and Recent Halimeda. In thin-section they show a medullary zone of coarse tangled threads (Pl. 23, fig. 1), and a cortex of approximately radial finer branching threads, whereas in Halimeda the central coarse threads are mostly longitudinally directed, and the cortical threads show constrictions and

swellings (Pl. 23, fig. 2). Steinmann (1899), in his comparison of the two, indicated a frequent triple branching of the swollen cortical threads of *Halimeda* as compared with a corresponding double branching of the slimmer *Boueina*-threads.

Arabicodium (type species: A. aegagrapiloides Elliott 1957, from the Lower Cretaceous of Arabia) occurs as slim cylindrical segments, occasionally showing incipient terminal branching. In thin-section they show a medullary zone of fine slightly wavy longitudinal threads, with cortical zones of very fine radially directed threads (Pl. 23, figs. 3, 4).

These two genera, well differentiated, both appear in the Jurassic and extend into the Lower Cretaceous. *B. hochstetteri liasica* was described from the Middle Lias of Morocco (Le Maitre 1937), and recorded from about the same level in Iraqi Kurdistan (Elliott 1960, and Pl. 23, fig. 1). In the Lower Cretaceous, besides the type-occurrence, there are Italian records of the species (Zuffardi-Comerci 1937) and of a variety *B. hochstetteri moncharmonti* (de Castro 1960). *Arabicodium* is recorded from the Middle Jurassic of France (Dufaure 1958), is known from the Upper Jurassic of Borneo, and has been seen from Tethyan Lower Cretaceous localities other than the type-locality.

In the Upper Cretaceous codiaceans are common: they have been referred variously to *Boneina* or *Halimeda*, but sometimes also resemble the later-described *Arabicodium*. Pfender (1940) listed various circum-Mediterranean Upper Cretaceous records and referred to the difficulty of allocating them to *Boueina* or *Halimeda*, though she recorded the definite occurrence of the latter from the Syrian Turonian. Pia (1936) described *Boneina pygmaea* from the Cenomanian-Turonian of Libya: it is a much smaller species than the type, and without the distinctive medullary threads. It has been recorded from the Cenomanian of France and Spain (Pfender 1940) and the Turonian of the Trucial coast, Arabia (Elliott 1960). In describing *Halimeda nana* from the Moroccan Danian Pia made the generic allocation on the occurrence of a branching segment and not on the internal structure, which was not well preserved (Pia, Pfender, and Termier 1932). Records of this species from the Palaeocene of the Middle East (Elliott 1955, 1960) are based on similarly small segments which, however, show a more markedly halimediform thread-structure than may be distinguished in the type-figures.

### EXPLANATION OF PLATE 23

Fig. 1. Boneina hochstetteri Toula var. liasica Le Maitre, longitudinal thin-section, ×28; coarse irregularly directed medullary threads, cortical threads mostly ill-preserved. Lower Jurassic, Sekhaniyan Formation (Middle/Upper Lias); Sekhaniyan, Surdash, Sulemania Liwa, NE. Iraq. Brit. Mus. (Nat. Hist.), Dept. Palaeont., V 51381.

Fig. 2. Halimeda praemonilis Morellet, longitudinal thin-section, ×28; coarse longitudinally directed medullary threads and characteristic cortical layer. Palaeocene, Sinjar Formation; Rowanduz,

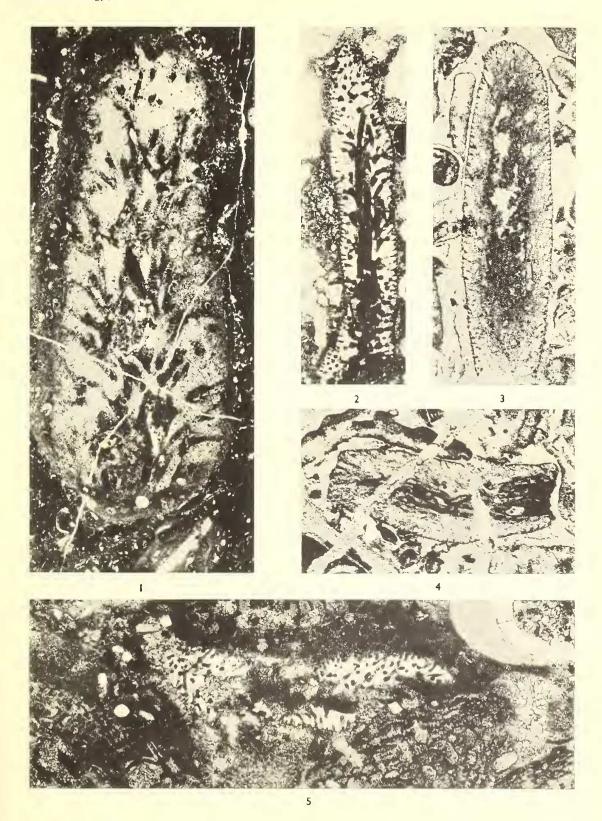
Erbil Liwa, NE. Iraq. V 41615.

Figs. 3, 4. Arabicodium aegagrapiloides Elliott, longitudinal thin-sections, ×28. 3, Outline and fine threads of cortical layer. 4, Distinctive fine longitudinally directed medullary threads. Basal Lower Cretaceous, Hugf area, Oman, Arabia. V 41625.

Fig. 5. Halimeda sp., random thin-section of damaged segment, ×40. Upper Cretaceous, Tanjero Formation (Maestrichtian); Balambo, Sulemania Liwa, NE. Iraq. V 51380.

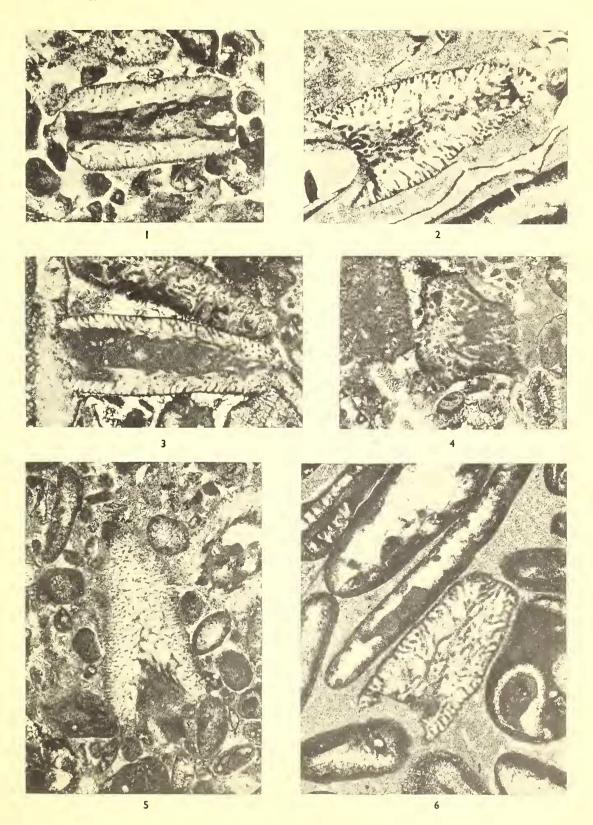
## EXPLANATION OF PLATE 24

Figs. 1, 3–5. Boueina spp., thin-sections, ×40. 1, 5, Upper Cretaceous (Cenomanian), Djebel Meketsi, Algeria. V 51383, V 51384. 3, 4, Lower Cretaceous (Upper Aptian), Ain Keiriane, Algeria. V 51382.
Figs. 2, 6. Boueina cf. pygmaea Pia, thin-sections, ×40. Upper Cretaceous (Cenomanian), Bou Saâda, Algeria. V 51385.



ELLIOTT, Mesozoic and Cretaceous Codiaceae





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